

寄主植物对植食性昆虫与昆虫杆状病毒互作的调控*

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摘要 植物与植食性昆虫、植食性昆虫与昆虫杆状病毒之间的两营养级互作关系, 至今已有超过半个世纪的研究历史, 但这三营养级的互作研究, 在近 20 年才引起科学家的兴趣。在查阅并理解国内外相关文献的基础上, 本文主要从植物的物理性状、营养物质和次生代谢物质三个角度出发, 剖析植物调控昆虫响应病毒感染的生态生理及免疫机制, 阐明植物影响病毒增殖、病毒组分及其感染过程和致病力的机理。此外, 本文就植物、植食性昆虫和昆虫杆状病毒互作的研究方向、研究方法, 进行了初步展望, 以期为更好研究多营养级共存系统的食物网关系, 提供理论依据。

关键词 植物; 次生代谢物质; 营养代谢物质; 植食性昆虫; 昆虫杆状病毒

The effects of host plants on the interactions between herbivorous insects and baculoviruses

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Abstract Although bi-trophic interactions between host plants and herbivorous insects, and between herbivorous insects and baculoviruses, have been studied for more than half a century, tri-trophic interactions have only attracted interest in the last two decades. Based on reviews of both domestic and foreign literature, we here describe the eco-physiological and immune mechanisms that insects use to respond to baculovirus infection, and elucidate the mechanisms that plants use to resist the pathogenicity of baculoviruses carried by host insects. We mainly focus on three aspects: plant physical characteristics, nutrient metabolites and secondary metabolites. Finally, we take a rough glance at the future of direction of research, and the kinds of tri-trophic interactions between plants, herbivorous insects and baculoviruses, in order to provide a theoretical basis for understanding the co-existence of multi-trophic groups in the food web.

Key words host plant; secondary metabolite; nutrient metabolite; herbivorous insect; insect baculovirus

长期以来, 植物、植食性昆虫与病原微生物的互作关系一直是生态学和生物防治的研究热点之一 (Shikano *et al.*, 2017a; Trębicki *et al.*, 2017); 在这三营养群 (Trophic group) 相互关系中, 寄主植物与植食性昆虫 (Wan *et al.*, 2020)、植食性昆虫与昆虫病原微生物 (Wan *et al.*, 2019; Chen *et al.*, 2020) 之间的互作, 已有系统深入

报道, 而寄主植物与昆虫病原微生物互作的研究相对较少。30 多年来, 科学家一直在搜集证据支持这样一个假说: 植物利用昆虫病原微生物作为防御因子来保护自身免受植食性昆虫的为害。Cory 和 Hoover (2006) 从三营养级相互关系的进化背景, 讨论了植物利用昆虫病原微生物充当“保镖”的机制, 认为寄主植物可以通过增加植

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食性昆虫对病原微生物的易感性来防御植食性昆虫。在自然界, 植物与昆虫病原微生物间是互利共生的关系, 这就要求植物能够影响昆虫病原体, 以抵御植食性昆虫取食带来的适合度损失; 植物能通过调控植食性昆虫的行为来增加病原体与植食性昆虫的接触机会 (Chandler *et al.*, 2011), 或通过改变自身的化合物调控植食性昆虫与其病原微生物的相互关系 (Cory and Hoover, 2006), 如植物的初级和次生代谢产物, 可以通过改变昆虫的免疫功能和病原体进入的物理屏障来影响昆虫与病原体相互作用的结果。有些昆虫利用植物的次生化学物质和营养物质来预防感染, 并通过这些药物来限制感染的严重程度。众多研究表明, 昆虫杆状病毒作为一类重要生防资源, 在控制虫害过程中扮演着重要角色, 因此立足于寄主植物与昆虫杆状病毒间的相互关系, 探索寄主植物如何与昆虫杆状病毒协同防御植食性昆虫, 对于高效利用杆状病毒防治害虫有重要意义。

在寄主植物、植食性昆虫、昆虫杆状病毒三

级营养层漫长的进化过程中, 各营养群之间形成了复杂的食物网 (Food web) 关系 (Shikano *et al.*, 2017a; Trębicki *et al.*, 2017), 直至最近 20 年, 植物、植食性昆虫和昆虫杆状病毒之间的三营养级互作关系 (Tri-trophic interactions), 才博得生态学家的注意 (Elliot *et al.*, 2000; Cory and Myers, 2004; Cory and Hoover, 2006; Shikano, 2017a)。在这三营养级中, 植物能调节植食性昆虫与昆虫杆状病毒的互作 (即上行控制) (Giron *et al.*, 2013; Spence and Bais, 2015), 昆虫杆状病毒也能调节植物与植食性昆虫的互作 (即下行控制) (万年峰, 2016; Wan *et al.*, 2017a), 其中对三者互作的上行控制研究已有较多报道。众多研究表明, 植物既影响病毒在宿主体内的增殖、病毒组分及其感染过程、感染性, 又能引起感毒宿主生理生态及免疫响应的变化 (Schenk *et al.*, 2008)。这里, 仅以昆虫杆状病毒或植食性昆虫为对象, 阐明植物调控昆虫与病毒互作的效应及其机制 (图 1), 旨在更全面理解多营养类群之间的食物网关系。

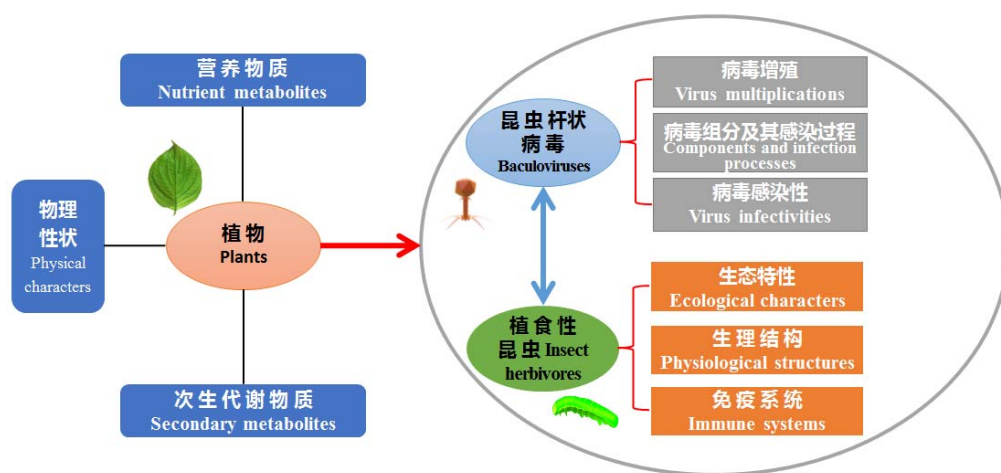


图 1 寄主植物对植食性昆虫与昆虫杆状病毒相互作用的调控

Fig. 1 Host plants regulate the interaction between insect herbivores and baculoviruses

1 植物对植食性昆虫与昆虫杆状病毒互作过程中病毒的调控

昆虫杆状病毒感染宿主是一个复杂的过程。多角体病毒被昆虫吞食后, 在宿主中肠的碱性环境中, 溶解释放包埋型病毒粒子 (Occlusion-

derived virus, ODV), ODV 与宿主肠道柱状上皮细胞细胞膜融合, 通过内吞体进入细胞进行复制 (Clavijo *et al.*, 2009; Iwata *et al.*, 2016)。病毒作用宿主的整个过程受植物调控, 主要体现在寄主植物会影响病毒在宿主体内的增殖、组分功能及其感染性。

1.1 病毒增殖

通常,昆虫杆状病毒经吸附、侵入、脱壳、生物合成、装配和释放等阶段,在宿主体内完成其增殖过程。植物通过直接或间接的方式影响这些阶段而调控病毒的增殖,如 Ali 等(2002)研究发现,核型多角体病毒经不同植物感染美洲棉铃虫 *Helicoverpa zea* 后,黄豆介导的病毒增殖量大于棉花。目前,植物对病毒增殖影响的可能机制研究主要集中在生态生化层面。从生态现象上分析,病毒增殖量取决于昆虫发育速率,而发育速率受寄主植物的影响;发育速率快的高龄感病毒主体内的病毒增殖量大,而生长缓慢的低龄宿主的病毒增殖量少(Raymond *et al.*, 2002; Thorne *et al.*, 2008; Bixby and Potter, 2010)。

病毒增殖量也与植物化学物质相关(Wang *et al.*, 2020)。昆虫取食高营养的含氮化合物和蛋白质后,会加速自身生长发育,个体快速增大(Raymond *et al.*, 2002; Vanbergen *et al.*, 2003)。病毒在以夏桉为食源的冬季蛾 *Operophtera brumata* 体内的增殖量,是以西加云杉为食源的 5 倍,这主要缘于夏桉叶片中含有较高的含氮量和蛋白质(Raymond and Hails, 2007)。可以理解的是,病毒复制依赖于昆虫宿主体内的营养物质,而昆虫的营养物质主要摄取于寄主植物。植物通过影响昆虫复制病毒所需的营养物质,间接调控病毒在宿主体内的增殖。一些研究表明,植物蛋白酶抑制剂(即丝氨酸、半胱氨酸和天冬氨酸)(Chandra and Pandey, 2008)、凝集素(Lectins)(Elden, 2000; 柴连琴等, 2014; Shahzad *et al.*, 2017)均可抑制昆虫的生长发育,表明植物也可通过次生代谢物质调控昆虫的生长而影响病毒增殖。

1.2 病毒组分及其感染过程

植物化学物质进入昆虫体内,首先影响病毒包涵体(Occlusion body, OB)释放病毒粒子。中肠的碱性环境促进 OB 释放病毒粒子(郑秦和吴小锋, 2016),因此植物叶片中自带的碱性离子进入昆虫中肠后,有助于提高 OB 释放病毒粒子的效率(Duffey *et al.*, 1995);其次,随着 OB

在宿主中肠液中的溶解,植物会进一步限制病毒蛋白质外壳的脱衣过程,主要体现在:植物叶片中的过氧化物酶(Foliar peroxidase)催化酚类物质氧化,植物酚类物质能与病毒包涵体形成聚集体,集聚成交叉结合的酚类蛋白壳,致使病毒无法释放衍生的包埋型病毒粒子(Occlusion-derived virus particles)(Felton and Duffey, 1990; Hoover *et al.*, 2000)。有研究表明,植物化学物质也可能影响病毒核酸复制和感染宿主的效率。历经脱衣过程后,病毒核酸从蛋白质外壳中“逃离”出来,继而感染宿主细胞,利用宿主细胞核中的营养物质组装蛋白。在病毒核酸复制和蛋白组装的过程中,植物凝集素可与病毒上的蛋白质配体发生特异性结合(Michiels *et al.*, 2010; 鲍锦库, 2011),干扰病毒核酸的复制、转录与翻译等一系列过程。植物凝集素与病毒识别受体结合后,通过竞争性抑制阻碍病毒对宿主的后续感染(鲍锦库, 2011)。可见,植物对病毒组分(包涵体、核酸和蛋白质壳)及其感染过程的调控是多方位的。然而,仍需在该领域回答更多的科学问题:究竟还有哪些(种)植物物质调控这些组分与功能、调控的机制是什么?

1.3 病毒感染性

评价病毒对宿主昆虫的感染力(Infectivity),一般用半致死剂量(LD₅₀)、半数致死时间(LT₅₀)、致死率等指标衡量(Peng *et al.*, 1997; Levy *et al.*, 2007; Stanley and Shapiro, 2007)。近 30 年来,植物调控病毒对昆虫的感染力颇受关注(Richter *et al.*, 1987; Salamouny *et al.*, 2003; Gasmi *et al.*, 2019),但主要集中在鳞翅目昆虫,代表性的有夜蛾科(Shikano *et al.*, 2010; Wan *et al.*, 2016, 2018)、尺蛾科(Raymond *et al.*, 2002)、枯叶蛾科(Cory and Myers, 2004)、舞毒蛾科(Bakhvalov and Bakhvalova, 2009)昆虫。实际上,这种感染力差异可以指导农业生产实践,即在利用昆虫杆状病毒进行害虫防治时,需根据不同作物上的病毒感染性差异合理使用病毒杀虫剂剂量(Monobrullah and Masao, 2000; Zhang *et al.*, 2011)。Wan 等(2016)研究发现,防治黄豆上的甜菜夜蛾 *Spodoptera exigua* 可用

较低剂量的核型多角体病毒,而防治薤菜、甘蓝和萝卜上的甜菜夜蛾则需用较高剂量的病毒。

理论上深究,病毒在不同植物上的感染力差异,与植物对病毒组分的影响程度以及对病毒复制后期感染的效果有关 (Hoover *et al.*, 1998a, 1998b; Wan *et al.*, 2018)。植物引起的病毒失活是病毒感染力减弱的直接原因 (Duffey *et al.*, 1995; Young *et al.*, 1995)。据报道,棉花叶片表面渗出的 Zn^{2+} 、 Mg^{2+} 、 Ca^{2+} 等碱性金属离子,通过与杆状病毒的蛋白发生沉淀作用而使病毒失活,而失活的病毒对美洲棉铃虫 *Helicoverpa zea* 的感染力下降 (Ali *et al.*, 2003)。同样,植物酚类物质通过与病毒的蛋白形成聚集物也能使病毒失活,进而降低病毒的感染力 (Young *et al.*, 1995; Ali *et al.*, 1999; Shapiro *et al.*, 2009)。研究证实,芸香苷 (Rutin)、绿原酸 (Chlorogenic acid) (Felton *et al.*, 1987)、水解丹宁 (Hydrolysable tannin) (Hunter and Schultz, 1993)、饮食丹 (Dietary tannis) (Young *et al.*, 1995)、印度黄檀苷 (Sissotrin) (D'Cunha, 2007)、七叶苷 (Esculin)、没食子酸 (Gallic acid) (Shapiro *et al.*, 2009) 等植物酚类物质对昆虫杆状病毒均有灭活效果。植物凝集素可能也是病毒感染力降低的重要因素 (Liang and Chang, 2002; Caccia *et al.*, 2012), 主要是因为植物凝集素是具有至少一个非催化结构域的蛋白质,可直接与昆虫杆状病毒的糖蛋白结合,干扰昆虫杆状病毒与宿主细胞的融合,截断病毒进入宿主细胞的途径,将病毒清除出宿主血淋巴。

其实,植物叶片中的一些活性酶也能增强病毒的感染力。近期研究发现,植物叶片中的氧化应激酶 (过氧化氢酶和超氧化物歧化酶),有助于增强昆虫杆状病毒的感染力 (Wan *et al.*, 2018)。该论点可从以下几方面阐释: 1) 病毒感染宿主后,诱导宿主细胞产生氧化应激反应,释放大量活性氧自由基;为了抵消氧化应激反应,宿主中肠细胞脱落,病死率增加; 2) 过氧化物酶的辅酶是 H_2O_2 ,用过氧化氢酶分解 H_2O_2 会降低过氧化物酶活性,即过氧化氢酶抑制过氧化物酶活性 (Shikano *et al.*, 2017b); 3) 活性氧自由

基作用下病毒复制和致病能力增加 (刘倩等, 2011),这是植物氧化应激酶诱导病毒感染性增强的一种合理解释。可见,植物对病毒感染力的作用具有正负两面性。

2 植物对植食性昆虫与昆虫杆状病毒相互关系中昆虫的调控

杆状病毒感染宿主后,会引起宿主昆虫生长发育、行为等生态特性 (Ishii *et al.*, 2002; Ordóñez-García *et al.*, 2019) 以及围食膜、中肠组织等生理结构 (Toprak *et al.*, 2012; Javed *et al.*, 2017) 的变化,也会诱导宿主产生细胞免疫 (Wan *et al.*, 2015a, 2015b; Silveira *et al.*, 2017) 和体液免疫 (Jiang *et al.*, 2013; Ji *et al.*, 2016; Wan *et al.*, 2017b)。当植物被摄入昆虫体内,会进一步影响宿主响应病毒的生态生理与免疫机制。

2.1 生态特性

昆虫感染病毒后,其生长发育受阻 (Ishii *et al.*, 2003; Detvisitsakun *et al.*, 2007)。当植物与病毒共同进入昆虫体内,植物的营养、次生代谢物质可进一步调控病毒对昆虫生长发育的抑制作用,且不同植物间的调控作用,也可能存在差异 (Shikano, 2017b)。植物介导下的感病宿主生长发育的差异,主要表现在发育历期和体重的变化。例如,紫叶生菜介导下的感毒烟芽夜蛾 *Heliothis virescens* 幼虫发育至 5 龄预蜕皮 (Premolt stage) 的时间,较棉花介导下的延长 2 d (Hoover *et al.*, 2000); 同样,相比于落叶松,山杏介导的感毒舞毒蛾 *Lymantria dispar* 的蛹期和发育历期也有延长的趋势 (朱丽春, 2008)。取食土耳其栎 *Quercus cerris* 的感毒舞毒蛾幼虫体重大于取食无梗花栎 *Quercus petraea* 的感病幼虫 (Schopf *et al.*, 1999); 与取食葛属 *Pueraria lobata* 鹿藿属 *Rhynchosia minima* 的夜蛾 *Anticarsia gemmatilis* 相比,取食大豆 *Glycine max* 和豇豆 *Vigna luteola* 的幼虫体重更大 (Peng *et al.*, 1997)。综合文献可知,植物化学物质抑制感毒宿主的生长发育,可能是通过抑制昆虫消

化蛋白酶 (Digestive proteinases) 实现的 (Telang *et al.*, 2009; Lomate and Hivrale, 2012)。至今已揭晓的该类植物化学物质包括: 几丁质酶 (Chitinase) (Gomes *et al.*, 1996)、蛋白酶抑制剂 (Proteinase inhibitors) (Jongsma *et al.*, 1995; Walz *et al.*, 2004; Hivrale *et al.*, 2013)、抗氧化防御蛋白 (Antioxidant defense protein) (Jovanović-Galović *et al.*, 2004; Huang *et al.*, 2008)、纯化氯化芍药素 (Purified peonidin chloride) (Johnson and Dowd, 2004)、大豆黄素 (Daidzein) (Zhou *et al.*, 2011) 等。

昆虫感染病毒后, 一般表现为反应迟钝、行动缓慢、觅食无力 (Jiang *et al.*, 2018; Wan *et al.*, 2019)。取食不同植物的宿主幼虫感染病毒后, 宿主的行为反应会因植物种类的不同而不同 (Erlandson *et al.*, 2007), 主要表现在以下几方面: 1) 取食行为的差异。这主要与植物的形态和生化特性有关 (王美芳等, 2009); 感毒粉纹夜蛾 *Trichoplusia ni* 幼虫在黄瓜叶片上的取食量是胡椒上的近 10 倍 (Sarfranz *et al.*, 2011), 主要归咎于: 相比于腺性 (Glandular) 毛状体 (Trichomes) 的胡椒叶, 该虫更喜好非腺性毛状体的黄瓜叶 (Choudhury and Copland, 2003); 此外, 面对胡椒中的辣椒素 (Capsaicinoids) 和黄瓜中的葫芦素 (Cucurbitacins), 该虫更能适应后者次生代谢物质 (Tallamy *et al.*, 1997)。2) 移动行为的差异。一是指感毒宿主在植株上不同部位间的分布差异, 这主要与病毒在植株上的分布特征有关 (Vasconcelos *et al.*, 1996; Goulson, 1997)。野外自然条件下, 植株顶部最易受阳光照射和雨水冲刷, 病毒最易失活, 这驱使植食性昆虫为避免病毒感染而逃向植株顶部 (D'Amico and Elkinton, 1995; Cory and Myers, 2003; Rebolledo *et al.*, 2015); 然而, 当植株上部被喷施过多的病毒后, 昆虫也会向偏向植株中部和下部移动 (Sarfranz *et al.*, 2011); 二是指感毒宿主在同一植株部位上移动距离的差异, 这主要取决于植物介导的病毒感染力强弱 (被感染程度越重, 宿主不安程度 (Restlessness) 越强烈、善活动), 例如, 以帚石楠为食源的感毒冬尺蠖蛾

Operophtera brumata 幼虫在切除茎 (Excised stems) 上平均每天爬行的距离, 分别是以夏栎和北美云杉为介导的感毒虫的 2 倍和 2.3 倍 (Raymond *et al.*, 2005)。3) 驱诱行为的差异。虽然, 我们未见植物释放的挥发物驱避或引诱感毒成幼 (若) 虫的案例, 但可以想象的是, 处于亚健康状态的感毒虫与健康虫一样, 嗅觉系统仍旧灵敏, 同样能响应植物挥发物的驱诱作用。现实生产实践中, 昆虫杆状病毒作为杀虫剂被喷施于植株表面, 通过影响植物释放的挥发物而间接调控植食性昆虫的驱诱行为。作者前期工作发现, 被喷洒在黄豆植株上的核型多角体病毒, 不影响黄豆释放的挥发物的种类, 但降低了黄豆释放的 (Z)-3-己烯-1-醇的相对含量, 且这种挥发物对甜菜夜蛾幼虫具有驱避效应 (万年峰, 2016)。毫无疑问, 一方面植物会直接影响感毒宿主的飞翔、交配等行为, 同时也会通过被喷洒的病毒间接调控昆虫的这些行为。

2.2 生理结构

围食膜是昆虫抵御病毒通过肠道进入其他组织的第一道生理屏障 (Terra, 2001; Jiang *et al.*, 2012; Chen *et al.*, 2020)。病毒感染破坏了昆虫围食膜结构的完整性, 进而加速了病毒粒子对中肠组织的感染 (Rao *et al.*, 2004; Kawakita *et al.*, 2015; 郭玲等, 2018a)。植物进入昆虫肠道内, 可直接作用于围食膜, 使围食膜增厚变大或变薄缩小, 进而抑制或加剧病毒对宿主围食膜的破坏。譬如, 与取食人工饲料的烟芽夜蛾 *Heliothis virescens* 幼虫围食膜相比, 取食棉花叶片的更厚, 而更厚的围食膜不利于病毒感染 (Plymale *et al.*, 2008)。首先, 植物叶片的物理性状, 可调控病毒对围食膜的作用。带刺坚硬性状的植物叶片钉刺在围食膜上, 破坏了围食膜的渗透性, 易加速病毒感染; 相反, 平滑柔软的叶片, 对围食膜结构和病毒的感染性影响不明显 (Keathley *et al.*, 2012)。其次, 蛋白质和蛋白聚糖 (Proteoglycans) 是组成昆虫围食膜的两大类重要物质 (Campbell *et al.*, 2008; Guo and Zhang, 2011), 进入昆虫体内的植物化学物质, 可促进

这些组分的化学合成,以增加围食膜的厚度和渗透性(Lehane, 1997)。再次,植物化学物质还可通过增加膜蛋白之间的交联或膜蛋白与几丁质骨架之间的交联,来巩固先前形成的膜结构(Plymale *et al.*, 2008)。最后,植物本身产生或者被诱导产生的栲酮(吕敏等, 2014)、单宁(Barbehenn, 2001)、几丁质酶(Jan *et al.*, 2008)、凝集素(Hopkins and Harper, 2001; Martinez *et al.*, 2012)等次生代谢物质,能够改变围食膜各组分的含量或渗透性,导致膜蛋白和几丁质的解离,进而使围食膜被病毒破坏更严重。

突破最内层的围食膜后,病毒粒子开始感染外层的肠壁细胞层,致使宿主中肠柱状细胞变形扭曲、细胞间隙变大凌乱、杯状细胞脱落变少、中肠肠壁增厚(卢晓等, 2009; 郭玲等, 2018b),最终诱发宿主消化道中肠上皮细胞的凋亡,并在释放病毒粒子进入血淋巴之前使被感染的细胞从中肠脱落(刘晓勇等, 2008; Hakim *et al.*, 2010; Liu *et al.*, 2011)。然而,在这个过程中,植物能够调控病毒诱发中肠细胞脱落的强度和进度,即中肠细胞形态变化越大、细胞数量脱落越多越快,植物介导的病毒对宿主的感染力越强(Volkman, 2007; Brits *et al.*, 2015)。例如,生菜介导的烟芽夜蛾对杆状病毒的易感性强于棉花介导的,归因于取食棉花的中肠柱状细胞的脱落率低于取食生菜的(Hoover *et al.*, 2000)。类似地,郭玲等(2018b)观察到,以黄豆为食源的感毒甜菜夜蛾幼虫的中肠细胞在感毒后 36 h 时细胞破裂,而以薹菜或甘蓝为食源的感毒幼虫在感毒后 48 h 出现这种现象,这验证了黄豆介导的甜菜夜蛾易感性强于薹菜和甘蓝介导的(Wan *et al.*, 2018)。昆虫中肠结构自内向外分别为围食膜、肠壁细胞层、底膜、环肌、纵肌和基底膜共 6 个部位,虽然植物介导的病毒对前两个部位的结构如上所述,已有详述,而对其他 4 个部位的探究,仍是未解之谜。可以推断的是,植物会用物理和化学两个“砝码”调控病毒对昆虫生理结构的影响。

2.3 宿主免疫功能

病毒突破宿主中肠组织的防御后,进入血淋

巴复制并进一步侵害宿主,随即面临的是宿主的细胞免疫和体液免疫(Siva-Jothy *et al.*, 2005)。在前一种免疫过程中,为抵御病毒感染,昆虫血细胞会产生凋亡(Wan *et al.*, 2015b)。植物影响感染病毒的昆虫细胞凋亡的差异及其分子机理,已得到部分证实,即取食薹菜和甘蓝的感毒甜菜夜蛾幼虫的细胞凋亡率显著大于取食黄豆的,较高的细胞凋亡率与较多的半胱天冬酶基因表达量、较少的细胞凋亡抑制子(Se-IAP)基因表达量有关(王金彦, 2019)。实际上,细胞凋亡是由多种蛋白(细胞色素 C、跨膜蛋白、钙粘蛋白、casepase 等)参与完成的信号转导反应(Liu *et al.*, 2012),包括接受凋亡信号、凋亡调控分子间的相互作用、蛋白水解酶的活化等几个阶段(Marmaras and Lampropoulou, 2009; Yamada *et al.*, 2012)。可以想象的是,植物化学物质可与这些蛋白发生拮抗或协同作用,共同作用于细胞凋亡的各个阶段。除细胞凋亡外,吞噬作用也是细胞免疫病毒感染的重要现象,主要由浆血细胞(Plasmatocytes)和颗粒血细胞(Granular cells)完成(Tojo *et al.*, 2000; Nardi, 2004)。遗憾的是,未见植物影响血细胞吞噬病毒的报道,但可以肯定的是,一方面植物有助于血细胞吞噬病毒,主要因植物化学物质(例如,酚类和碱性离子)通过灭活病毒而使病毒结构解离;另一方面,植物也可影响昆虫的生长发育,生长发育的速率制约昆虫血细胞组成结构,这也是植物调控血细胞吞噬病毒的重要原因。

黑化反应是昆虫免疫病毒感染的重要途径。昆虫感染病毒后,其血淋巴黑化程度降低(Yuan *et al.*, 2017)。取食不同植物的宿主昆虫,感毒后的黑化反应存在差异,且这种差异决定宿主对病毒的免疫能力。例如,以黄豆为食源的感毒甜菜夜蛾幼虫黑化率明显低于以薹菜和甘蓝为食源的,这表明取食薹菜和甘蓝更有利于宿主抵抗病毒的感染(王金彦等, 2018)。归根结底,植物介导的感毒宿主黑化反应的强度,受控于参与黑化反应的关键酶以及影响这些关键酶合成的基因表达。Wang 等(2020)进一步验证发现,黑化反应率与 3 种黑化反应关键酶(多酚氧化

酶、酪氨酸羟化酶和多巴脱羧酶)活性、黑化反应关键酶基因表达量均呈正相关关系,取食黄豆的感毒甜菜夜蛾幼虫的低黑化反应率与其较低的黑化反应关键酶活性、较少的黑化反应关键酶基因的转录水平有关。除以上3种酶外,参与宿主体液免疫反应的还包括溶菌酶、抗菌肽等多种酶。遗憾的是,这些酶与黑化反应的关系鲜见报道。可以推理的是:一方面,植物本身的一些酶(如过氧化物酶)可催促植物酚类灭活病毒,进而有助于昆虫对病毒的体液免疫;另一方面,植物释放的次生代谢物质(如蛋白酶抑制剂),通过抑制昆虫生长发育而减弱宿主对病毒的免疫能力。

3 结语与展望

综上所述,植物既能调控病毒在宿主体内的增殖、感染过程以及感染力,又能调控感毒宿主的生理生态以及免疫反应。然而,该方面的研究主要集中在受控的实验室研究(Controlled laboratory experiments),很少涉及野外试验(Raymond and Hails, 2007; Elder et al., 2013)。就研究方法而言,该方面的研究需要从微观分子和宏生态学(Macroecology)领域加以更多阐释。随着基因组学、蛋白组学、代谢组学、全球变化生态学等新型学科的发展,作者相信这些手段会被逐渐应用到植物对昆虫与病毒互作的调控机制研究中。此外,在“植物-植食性昆虫-昆虫杆状病毒”三营养级互作关系中,昆虫杆状病毒对植物与植食性昆虫间互作的调控效果及其机制的研究,也应引起足够重视。可以预见的是,不同昆虫杆状病毒的感染,可引起虫害诱导的植物挥发物以及一些植物次生代谢物质的变化,也可导致昆虫取食植物后生理生态特征以及免疫系统的差异。

目前,科研人员对植物调控植食性昆虫与昆虫病毒互作的认识,尚处于初级阶段。首先,植物含有多种物理性状、营养物质和次生代谢物质,虽然我们能够对每种性状或物质的功能进行单独测试,但是这些性状和物质对昆虫与病毒互作过程中的协同或拮抗机制,尚不清晰。其次,

植食性昆虫取食植物后,会导致植物防御信号分子(如水杨酸、茉莉酸和乙烯)水平的增加并且伴随着特定的防御相关基因的激活(Reymond et al., 2000),这些防御信号分子及其相关基因表达如何影响昆虫与病毒的互作,亟待探索。最后,迄今绝大部分实验材料来自于室内繁殖多代的昆虫群体、单一的植物品种和单一品系的昆虫杆状病毒,植物品种的种内遗传变异如何影响昆虫与病毒的互作关系,有待进一步探讨。

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